

ECOLOGY OF TWO ASCLEPIAD LIANES IN SEMI-ARID VICTORIA

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Marsdenia australis and *Rhyncharrhena linearis* (Asclepiadaceae) are lianes of the "thin wiry" type. In Victoria they are found in semi-arid woodlands, secondary shrublands and mallee communities. Both can sucker profusely from the roots to form large clones but only *Marsdenia* has tuberous roots. Both species have a pair of foliar glands per leaf adaxially at the leaf base.

Fresh seed of both species has high germinability and most germinated in a few days, especially at 25°C. Germinability of *Marsdenia* seed declines with time and is zero at 14 yr. At 18 weeks old, *Marsdenia* seedlings have higher dry weights than those of *Rhyncharrhena* due to their well-developed tuberous root systems.

Although both species flower annually, there is regular November–December *Marsdenia* flowering, even in very dry conditions, whereas only a few *Rhyncharrhena* flowered after heavy rain within the January–April period during our study. Fruit set was low for both species, especially *Rhyncharrhena*. Both species showed some increase in shoot length from February to September; this is most rapid when rain falls during warm weather. During drought, *Rhyncharrhena* plants rapidly lost leaves while *Marsdenia* plants did not. Tuberous roots may allow *Marsdenia* to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Both species are now vulnerable in Victoria. It is thought that the main threat is grazing by stock and rabbits. Fruiting has only been seen in plants which are climbing above 0.5 m in shrubs or trees; deliberate introduction of long-lived woody plants is needed to ensure seed production of *Marsdenia* and *Rhyncharrhena* in some grazing enclosures.

THE ASCLEPIADACEAE is a predominantly pan-tropical family of about 2000 species, mostly of woody climbers, perennial herbs and shrubs. The 60-odd Australian species occur mainly in the east and north, especially in rainforest, but a few species are widespread in semi-arid to arid areas and reach temperate latitudes (Williams 1984). Of the 12 or so important dicotyledonous liane families, Asclepiadaceae and Convolvulaceae (see below) are two which especially spread beyond rainforests into seasonally dry areas, both in Australia and elsewhere (Forster 1988, Hegarty 1989, Vahrmeijer 1981).

Lianes show decreasing robustness with decreasing annual rainfall; those dealt with here belong to the most slender of Webb's (1978) liane categories, being normally present as the "thin wiry" type (stem diameters less than 10 mm). In semi-arid north-western Victoria, there are seven native species which could be considered under this heading: *Marsdenia australis* and *Rhyncharrhena linearis* (Asclepiadaceae), *Jasminum didymum* ssp. *lineare* (Oleaceae), *Clematis microphylla* (Ranunculaceae) and

Convolvulus crispifolius, *C. erubescens* and *C. remotus* (Convolvulaceae). Species nomenclature follows Ross (1990) except that the name *Marsdenia australis* (R. Br.) Druce has been preferred to *Leichardtia australis* R. Br. following recent revisionary studies suggesting that *Leichardtia* is a synonym of *Marsdenia* (P. I. Forster personal communication). Inclusion of the *Convolvulus* spp. on the above list may be contentious as similar *Convolvulus* species are treated by some authors as herbaceous, not woody, climbers (Pate & Dixon 1982, Keeley & Keeley 1988).

Of Australian asclepiads, only a small number of species from *Cynanchum*, *Marsdenia*, *Rhyncharrhena* and *Sarcostemma* occur in semi-arid to arid regions. They show various features thought to be xeromorphic, like leaflessness and succulence (*Sarcostemma*) or reduced leaves (e.g. *Rhyncharrhena*) (Lapinuro 1976). The only such species occurring in Victoria, to be dealt with in detail below, are *Marsdenia australis* and *Rhyncharrhena linearis*. Other than these, the only native asclepiads in Victoria are



Fig. 1. Fruiting *Marsdenia australis* growing on *Dodonaea viscosa* at site 3 in March 1991.

two species of *Marsdenia* and one of *Tylophora* in the rainforests and adjacent tall open-forests of East Gippsland 600 km to the south-east.

The aim of this paper is to provide an introduction to the ecology of two asclepiads of arid and semi-arid areas, *Marsdenia australis* (Fig. 1) and *Rhyncharrhena linearis* (Fig. 2), at the temperate, southern limit of their range in Australia. *Rhyncharrhena* is one of only four asclepiad genera endemic to Australia, while *Marsdenia* is one of the most widespread genera, extending through parts of Asia, Africa and America. It is assumed that both *M. australis* and *R. linearis* were derived from northern Australian rain-forest taxa in response to increasing aridity (Beadle 1981).

The work, nearly all in Victoria, is based on sporadic field observations from 1981 to 1989 and intensive work from January to December 1990. For brevity, the species will be referred to simply by their generic names. Two reasons for the project are (1) that both species have a con-



Fig. 2. Fruiting *Rhyncharrhena linearis* growing on *Dodonaea viscosa* at site 1 in March 1991.

servation status rated as vulnerable Victoria-wide (Gullan, Cheal & Walsh 1990) so that data are needed as a basis for their management, and (2) that both were important aboriginal foods (Latz 1982) and *Marsdenia* in particular may be worth cultivating for its palatable fruits and its use as an indoor plant (Cherikoff & Isaacs no date, V. Cherikoff personal communication).

DISTRIBUTION AND HABITAT

Both species occur in inland parts of all mainland states of Australia including Queensland (Cunningham et al. 1981, Queensland Herbarium unpublished). There are records of both from at least as far north as 20°S, about the latitude of Tennant Creek (P. Latz personal communication) to as far south as 35°S near Walpeup in northwestern Victoria (this study).

Mean annual rainfall for both species can range from below 150 mm in the Great Victoria Desert (Greenslade, Joseph & Barley 1986) to above 400 mm in central New South Wales (Wilson 1980, Royal Botanic Gardens Sydney 1989). Seasonal rainfall distribution shows a slight May to October peak in Victoria (Badawy 1982) but changes to a summer maximum which becomes progressively more marked northwards (Slatyer 1962).

The whole area experiences hot summers and mild winters; mean temperatures increase steadily northwards. While frosts are very rare to absent north of 21°30', mean annual frost frequency ranges from 7 to 32 in the area from Alice Springs to northwestern Victoria without correlating closely with latitude (Slatyer 1962, Australian Bureau of Meteorology unpublished data). Mean length of frost season is more

strongly related to latitude, reaching a maximum of 109 days in the south of the area in northwestern Victoria (Australian Division of National Mapping 1986, Badawy 1982). Given the recent emphasis on absolute minimum temperature in defining distribution limits (Woodward 1987, Booth 1990), such values range from 4.5°C at Tennant Creek, -7.5°C at Alice Springs, -2.8°C at Broken Hill, -4.0°C at Mildura, -5.8°C at Ouyen and -2.0°C at Walpeup (Australian Bureau of Meteorology unpublished screen temperatures).

Within the area studied in detail, northwestern Victoria, mean annual rainfall increases from 250 mm in the north (Neds Corner) to 343 mm in the south (Walpeup). Temperatures decrease and frost season increases at the same time; the areas south of about 35°S lacking *Marsdenia* and *Rhyncharrhena* are both wetter and colder than those areas supporting them (Badawy 1982). As growth of both species occurs especially in summer, decreased summer rainfall could possibly limit their distribution. However, there is no such decrease going from the north to the south of their Victorian range; some factor related to declining temperatures seems more likely to set their southern limits.

There is no clear evidence that the two species differ in their climatic tolerances.

A survey in 1985-6 of 1,300 20 m × 20 m quadrats in predominantly native vegetation in northwestern Victoria produced four records of *Marsdenia* and eight of *Rhyncharrhena* (Cheal & Parkes 1989 and personal communication), so these are not common species.

The Victorian distribution maps show 23 *Marsdenia* minor grid records and 15 of *Rhyncharrhena* (Fig. 3), partly reflecting the view that *Rhyncharrhena* is much the rarer of the two, e.g. in Victoria (J. N. Macfarlane personal communication) and around Broken Hill (Morris 1975).

In central Australia, most *Rhyncharrhena* plants are found in *Acacia aneura* communities, while *Marsdenia* occurs in most habitats (P. K. Latz 1982 and personal communication). However, in New South Wales both species occur in a wide range of communities, including those dominated by *Acacia aneura*, *Casuarina pauper*, *Eucalyptus intertexta* and various mallee species of eucalypt ("mallee") (Cunningham et al. 1981). In Victoria, the two asclepiads have very similar habitat ranges, both occupying relatively fertile sandy loams to clay loams carrying (1)

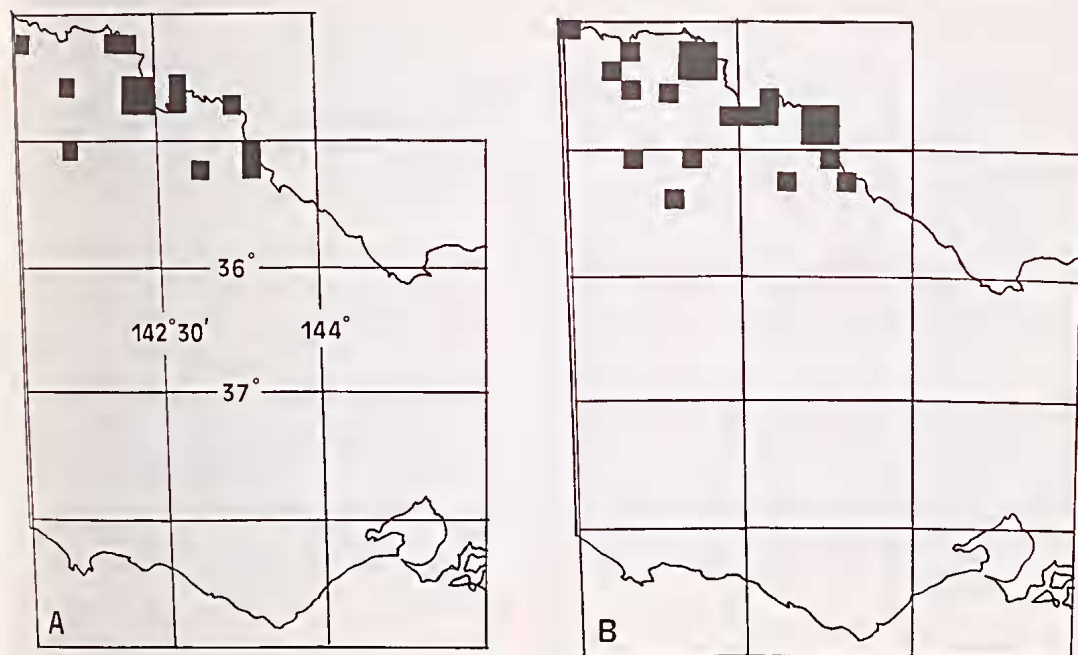


Fig. 3. Victorian distribution of (A) *Rhyncharrhena linearis* and (B) *Marsdenia australis* based on presence or absence within 10° latitude × 10° longitude grid squares for post-1950 records. All records from the Flora Survey and Management Group, Department of Conservation and Environment, with the addition of A31 and F29 for *M. australis*.

Site	Location ¹ /management	Mean annual rainfall ² (mm)	Area ⁴	Topsoil texture	Plant community	No. of shoots seen in 1990 adults/suckers	
						M	R
1	Department of Agriculture land, Campbell Avenue, Red Cliffs	285	8 ha	Sandy loam	<i>Cassia nemophila</i> - <i>Dodonaea viscosa</i> low shrubland ³	22/20	39/70
2	Red Cliffs Scenic Reserve	285	21 ha	Sandy loam	<i>Cassia nemophila</i> - <i>Maireana pyramidata</i> low shrubland ³	1/20	10/20
3	Red Cliffs Primary School Conservation Area	285	2 ha	Sandy loam	<i>Casuarina pauper</i> - <i>Callitris preissii</i> low woodland	9/15	3/10
4	Hattah-Kulkyne National Park	305	M 800 m ² R 225 m ²	Sandy loam	<i>Eucalyptus socialis</i> tall shrubland	1/10	1/100
5	Walpeup Flora & Fauna Reserve	343	50 m ²	Sandy clay loam	<i>Eucalyptus dumosa</i> open scrub	13/20	None
6	Pink Lakes State Park	312	M 1156 m ² R 1 ha	Sandy loam	M - Semi-cleared <i>Callitris preissii</i> low woodland R - Semi-cleared <i>E. socialis</i> tall shrubland	2/25	0/22

Table 1. Characteristics of Victorian *Marsdenia* and *Rhyncharhena* sites examined in detail. ¹ See Appendix 1 for details. ² Using values from the Red Cliffs, Hattah, Walpeup and Underbool stations. ³ Secondary shrublands following clearance of woodlands like those at site 3. ⁴ M = *Marsdenia*, R = *Rhyncharhena*.

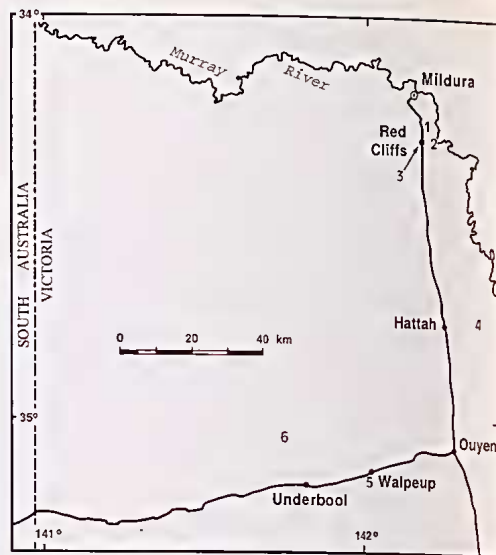


Fig. 4. Location of the study sites in north-western Victoria.

woodlands of *Casuarina pauper* and/or *Callitris preissii*, (2) various mallee communities or (3) various secondary shrublands following disturbance of (1) or (2) (see Table 1). They appear to be absent from the relatively infertile deep sands and from floodplains.

Sites for detailed study (Fig. 4) were chosen to encompass a range of mean annual rainfalls (Table 1, Appendix 1) and to include the largest populations known to us (sites 1, 3 and 5), as well as populations exclosed against grazing mammals in conservation reserves (sites 4 and 6).

MORPHOLOGY

Seed and seedling morphology

Marsdenia seeds are glabrous, dull, mid-to dark brown, flattened, finely winged, pyriform to ovate and comose at the narrower, germinating end. Germination is epigeal, the radicle emerging a minimum of two days from imbibition. Many short, fine root hairs develop as the radicle elongates (Fig. 5). The testa usually falls away in one piece. Sometimes it fails to fall off and dries, in which case it must be removed to allow seedling development as is the case in some other asclepiads (Harp 1987). The cotyledons are flat, petiolate and elliptical to obovate (Fig. 5). Tri-cotyledony occurs occasionally.

At 18 weeks, all seedlings have a tuberous taproot typically 10 mm in diameter with fine

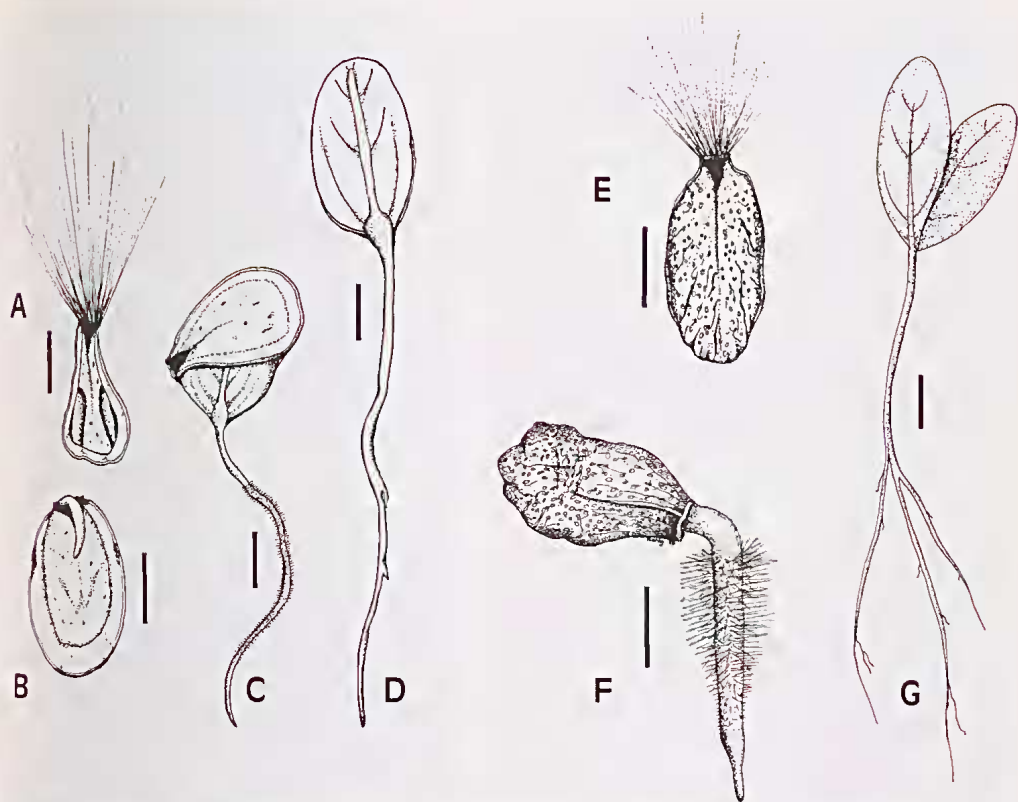


Fig. 5. Seeds and young seedlings of *Marsdenia australis* (A-D) and *Rhyncharrhena linearis* (E-G). A, E, dry seeds with comas. B, seed with radicle 2 days after sowing. C, F, seedlings 7 days after sowing showing root hairs. D, G, seedlings 12 days after sowing. Scale bars = 3 mm.

secondary roots (Fig. 6A) when the shoots are 440 mm tall.

On exceeding about 150 mm in height, the stem is unable to support the weight of the expanding leaves and bows over to become nearly horizontal; lateral shoots then develop from lower nodes. At this stage, the distal part of shoots can begin to revolve dextrorsely and to twine around any support encountered. Without support, the stem may bow almost to the ground and twine up about itself.

Rhyncharrhena seeds are rugulose, dull brown, flattened and elliptical to oblong. Germination and young seedling morphology are as for *Marsdenia* except for longer, denser root hairs and narrow-elliptical cotyledons (Fig. 5). No problem with persistent testas was found.

At 18 weeks, a root system lacking tubers is present (Fig. 6B); stem growth is similar to *Marsdenia*. There is no obvious ontogenetic change in leaf shape in either species.

Adult morphology

Shoots. Both species have opposite leaves lighter green and with denser stomata on the abaxial than on the adaxial surface. The stomata are modified rubiaceous type (Metcalf & Chalk 1957).

Stem diameter was typically 5–7 mm and up to 10 mm in *Marsdenia*, but only 3 to 5 mm in *Rhyncharrhena*. When no support is found by circumnating stems of either species, the stems can twine around themselves. In *Marsdenia* this can result in tightly plaited ropes up to 6 m long (Fig. 7); similar stems occur in the asclepiad *Araujia sericofera* (Menninger 1970).

Like most Australian asclepiads, *Marsdenia* and *Rhyncharrhena* are apical stem twiners, a type of behaviour said to be seldom effective in climbing trees of over 100 mm diameter at breast height (Hegarty & Clifford 1984). In this study, we found them twining up a range of

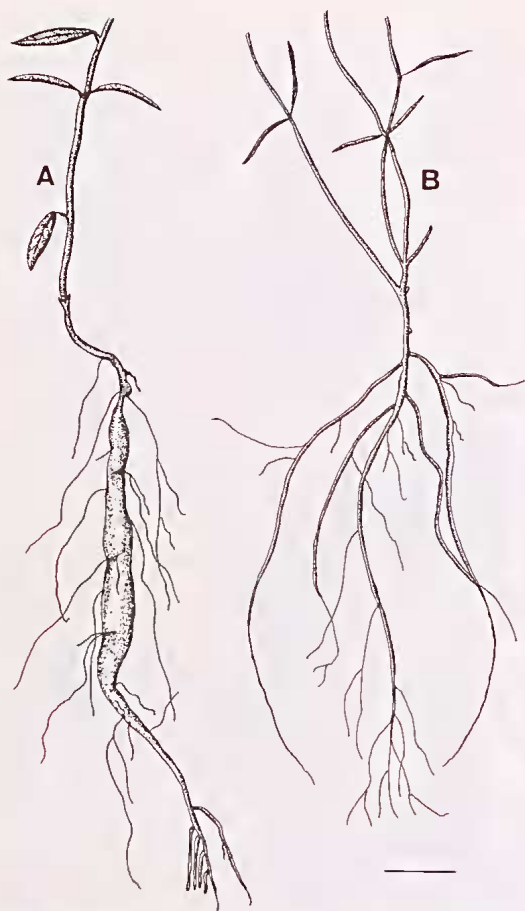


Fig. 6. Eighteen-week-old seedlings of (A) *Marsdenia australis*, showing tuberous taproot and (B) *Rhyncharrhena linearis* with non-tuberous roots. Scale = 20 mm.

shrubs and mallee eucalypts, with *Marsdenia* twining up eucalypt trunks of up to 90 mm diameter and to heights of at least 4 m. Where *Marsdenia* and *Rhyncharrhena* occurred in *Callitris-Casuarina* woodlands, we found them on shrubs but not on the trees. While there are records from large trees (e.g. photograph of *Rhyncharrhena* on *Callitris*, Victorian reference set, National Herbarium of Victoria), it may be that such trees were climbed many years previously when they had thinner stems.

Internode lengths were shorter for unsupported lianes than supported ones and were generally shorter for *Marsdenia* than for *Rhyncharrhena*. It was common to find small, unsupported shoots scattered in the vicinity of large, supported plants in both species.



Fig. 7. *Marsdenia australis*. A plait of five stems 35 mm in diameter at site 5; the plant extends from the soil surface to the crown of a mallee species of *Eucalyptus* (stem visible in background).

Roots and perennation. Parts of site 1 were excavated on 26–27 June 1990 to determine whether small, unsupported shoots were suckers or seedlings, and simultaneously to describe root systems.

Excavation of one adult *Marsdenia* plant and ten small shoots in an area of 2×1.5 m showed that all ten were suckers. Tissue sections showed that these arose from lateral roots. The suckers were from roots at depths of 100 mm to more than 500 mm below the surface and with diameters of 5 to 18 mm (Fig. 8A–C). They can occur more than 2 m from the parent plant.

Marsdenia has perennial tuberous roots, both laterals and tap-roots, the laterals up to 0.5 m long and 25 mm in diameter (Fig. 8A–C) and thus appreciably larger than those recorded in this species by Pate & Dixon (1982). The tuberous roots contain many large starch grains up to 10 μ m in diameter; the stems have fewer, smaller grains (2.5 μ m diameter). Copious branching leads to a complex system of tuberous

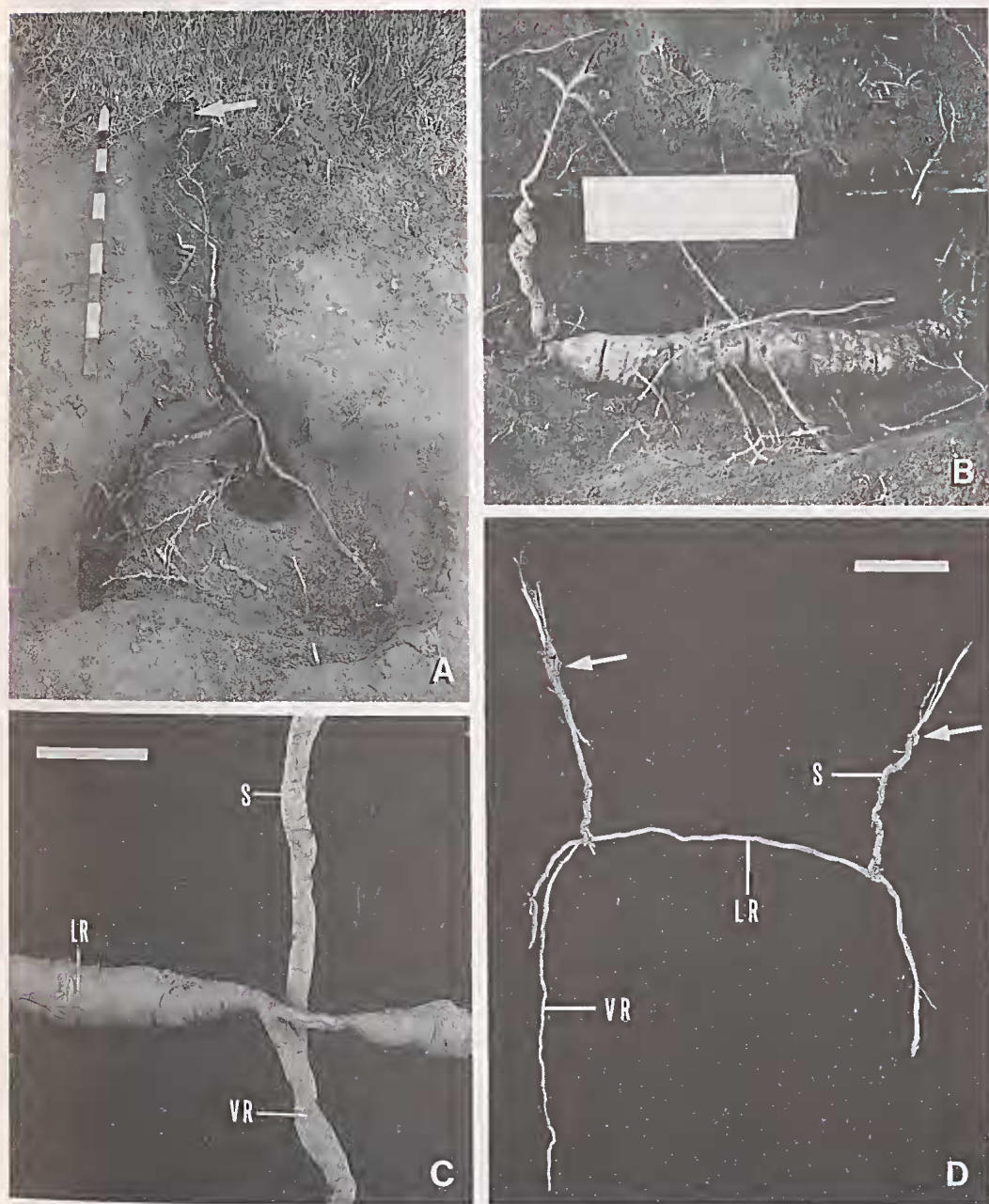


Fig. 8. A, partly-excavated root system of *Marsdenia australis* at site 1, showing tuberous horizontal and vertical roots. Arrow shows stem of adult plant. Scale divisions = 100 mm. B, part of *Marsdenia australis* plant at site 5, showing sucker shoot and tuberous root of 18 mm diameter. Scale divisions = 100 mm. C, part of *Marsdenia australis* plant at site 1 showing stem of sucker shoot (S), vertical root (VR) and tuberous root (LR) about 200 mm below soil surface. Scale = 30 mm. D, part of *Rhyncharrhena linearis* plant at site 1 showing two sucker shoots, stem (S), lateral root (LR), level of soil surface (arrow) and vertical root (VR). Scale = 50 mm.

roots in a number of layered, horizontal planes (Fig. 8A). Lateral tuberous roots were seen from 100 to 500 mm below the soil surface; vertical tuberous roots continued beyond 750 mm.

Tuberous roots are common in a number of liane families including the Asclepiadaceae, especially in species from seasonally dry areas rather than those from undisturbed evergreen rainforest (Hegarty 1989, Janzen 1975). Asclepiad examples include various African species of the succulent genus *Ceropegia* (Jacobsen 1960) and the Australian *Marsdenia flavescens*, *M. leptophylla* and *M. viridiflora* (Williams 1984).

Excavation of three small *Rhyncharrhena* shoots in an area of 500 × 200 mm showed them to be suckers, again from lateral roots (proved by tissue sections). Unlike *Marsdenia*, *Rhyncharrhena* roots are thin (diameter rarely greater than 5 mm) and non-tuberous, the laterals are not found deeper than about 200 mm and there is little branching (Fig. 8D). Starch grains are absent from the roots but present in the stems as before. Lines of sucker shoots strongly suggest that lateral roots can extend more than 15 m from parent plants (Fig. 9).

Root suckering, recorded here in *Marsdenia* and *Rhyncharrhena*, is known in other asclepiads, e.g. in *Morrenia odorata* (Tucker & Phillips 1974) and *Asclepias syriaca* (Bhowmik & Bandeen 1976) which can form clones of several thousand stems (Wilbur 1976). Such suckering may be "the most conspicuous form of

asexual multiplication" in tropical perennials and may, for all we know, produce very large individual plants of great longevity, each spread over many hectares (Janzen 1975). Such suckering may allow some liane individuals, including *Marsdenia laxiflora*, to persist more or less indefinitely in the absence of regeneration from seed (Penalosa 1984). Other aspects of suckering are dealt with later.

Without data on root depth limits and location of soil moisture reserves, we are unable to classify *Marsdenia* and *Rhyncharrhena* root systems into types. Clearly both have extensive lateral roots. *Marsdenia* roots extend beyond 750 mm deep and Pate & Dixon (1982) treat the species as deep-rooted, but further data are needed.

ANATOMY

Methods

Seedling tissue 18 wk old was fixed in 5% glutaraldehyde in phosphate buffer, dehydrated in a graded ethanol series and then infiltrated with LR White resin ('BioRad' Microscience Division, Hemel Hempstead) over 72 hr and polymerized at 65°C overnight. Thick sections were obtained using an American Optical Corp. Model 860 sledge microtome and stained with 1% safranin (aqueous).



Fig. 9. *Rhyncharrhena linearis* sucker shoots marked with flags at site 4. Mature plant from which the suckers are probably derived is approximately 10 m to the left of the photo inside the fenced plot.

Stem

The stems of *Marsdenia* and *Rhyncharrhena* have a continuous vascular cylinder traversed by narrow rays (Fig. 10) as in many other asclepiads (Metcalf & Chalk 1957). Both species have simple uniseriate hairs (Fig. 10A) and many druses attached to the wall of cortical cells (Fig. 10B). The cells of the hypodermis look very similar to those of the epidermis in both species.

Phloem occurs as small strands internal to the primary xylem (Fig. 10) in both species; such intraxylary phloem is universal in the family (Metcalf & Chalk 1957). Some vessel elements have larger diameter in *Rhyncharrhena* than in *Marsdenia* (Fig. 10). Both species have thick-walled fibres adjacent to the external phloem. In both, broken cells indicate the natural disintegration of the central pith to produce a lysigenous cavity (Fig. 10).

While laticifers are thought to occur in the shoots of all asclepiads (Metcalf & Chalk 1957), they can be difficult to distinguish (Metcalf 1966) and we were unable to identify any with certainty. Cut stems exude milky latex in *Marsdenia* as in most asclepiads, but not in *Rhyncharrhena* which we assume has watery latex as seems to occur in *Asclepias tuberosa* (Wilbur 1976), *Ceropegia cumingiana* (Bruyns & Forster 1989) and some other asclepiads (Williams 1984).

Foliar glands

A number of plant species including asclepiads have foliar glands or squamellae adaxially at or near the leaf base (Ramayya & Bahadur 1968). As their nature in asclepiads is almost unknown, they were examined in *Marsdenia* and *Rhyncharrhena*.

Both *Marsdenia* and *Rhyncharrhena* have a pair of glands per leaf adaxially at the leaf base (Figs 11, 12). The glands are up to 0.3 mm long and exude copious amounts of a sticky, transparent substance through a large pore in the centre of the gland head (Fig. 11). Both stalk and head are nearly cylindrical but are more convex abaxially; the head sits obliquely on the stalk. Vascular tissue is absent. Necrotic cells on gland tips of older leaves may show that glands gradually cease to function once the leaves mature (see also Lapinuro 1976).

In the closely-related Apocynaceae, the gland secretion is thought to be a high polymer resin and its suggested role is to provide a protective coating on adjacent young lateral buds

(Ramayya & Bahadur 1968); this may apply also in *Marsdenia* and *Rhyncharrhena*. Such coatings might protect against climatic extremes in arid areas (Dell & McComb 1978) or against herbivores (Juniper & Jeffree 1983).

The anatomy and morphology of the glands are very similar to those of the other taxa examined in detail, both Apocynaceae (Ramayya & Bahadur 1968) and the asclepiad *Marsdenia liisae* (Lapinuro 1976, Williams 1989).

GERMINATION

Methods

The coma was removed from seeds of known age and provenance (Appendix 2) and any broken, shrivelled or empty seeds discarded. Seeds were surface sterilized in 3% sodium hypochlorite and sown onto 9 cm Whatman 182 filter papers in sterile glass petri dishes, with five replicates of ten seeds per dish. The dishes were placed in growth cabinets with lights supplying 180–240 $\mu\text{E m}^{-2} \text{s}^{-1}$ for a 12 hr photoperiod at 10/10°C, 16/14°C, 25/15°C and (*Marsdenia* only) 30/20°C. For *Marsdenia* only, seed of four ages (Appendix 2) stored at room temperature and humidity was tested for germinability at 25/15°C. Comparable *Rhyncharrhena* seeds were not available.

Results and discussion

No seeds germinated at 10/10°C. For *Marsdenia*, final germination percentage was very similar at 25/15°C and 30/20°C but the germination rate was faster at 25/15°C. By comparison, 16/14°C reduced both the amount and the rate of germination in both species. Germination was highest and fastest in *Rhyncharrhena* at 25/15°C (Fig. 13).

Germinability of *Marsdenia* seed declined steeply with time and was zero at 14 yr (Fig. 14).

The germination maximum of 25/15°C for *Marsdenia* is broadly similar to that for other asclepiads like *Morrenia odorata* (20–25°C; Singh & Achhircddy 1984) and *Ampelamus albidus* (30°C; Soteres & Murray 1981). The present data for 10/10°C and 16/14°C suggest that germination may be reduced or prevented by winter temperatures in the field. All viable seeds of both species tend to germinate quickly given appropriate conditions; there is no evidence of dormancy as in some cool temperate species like *Asclepias syriaca* (Bhowmik & Bandeen 1976).

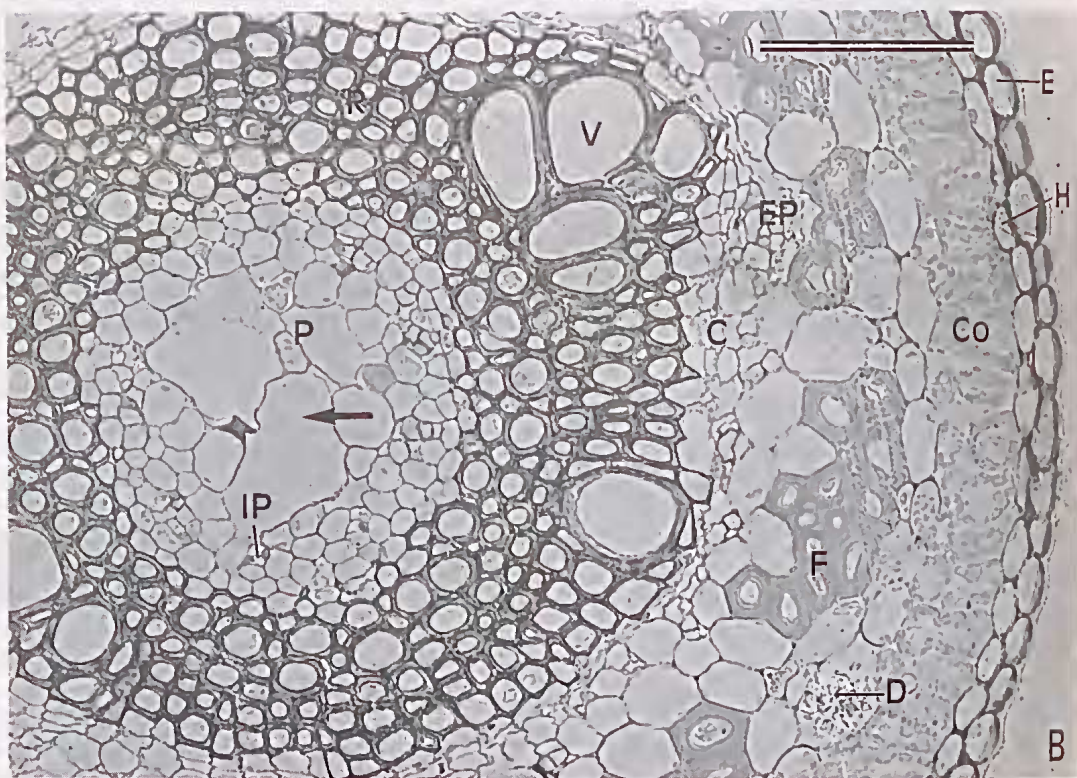
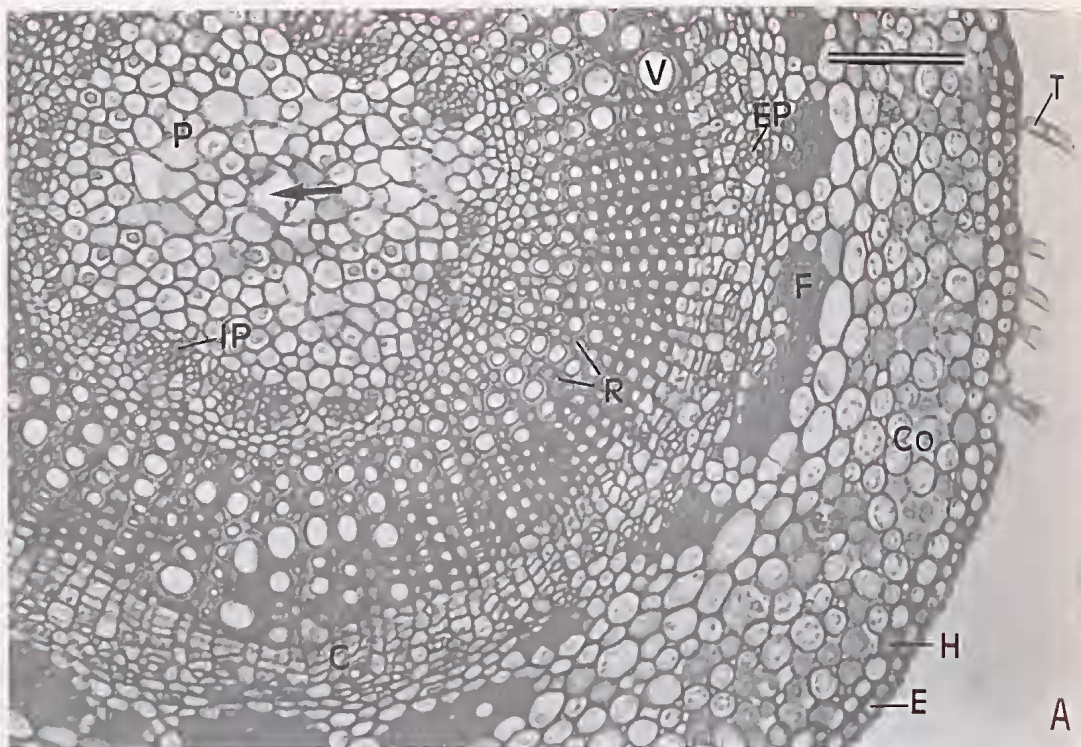


Fig. 10. Transverse sections of lower stems from approximately 18 week-old plants of *Marsdenia australis* (A) and *Rhyncharrhena linearis* (B), showing thick-walled epidermis (E) and hypodermis (H), trichome (T; cut short in sectioning), cortical chlorenchyma (Co), a druse (D), external phloem (EP) and phloem fibres (F), secondary xylem with vessels (V) and thickened rays (R), internal phloem (IP) and pith (P) with lysigenous cavities (arrowed). Scale bars = 0.1 mm.

The fast germination found here is similar to that found for a range of dry-country succulent asclepiads (Harp 1987).

SEEDLING GROWTH

Methods

Seedlings 5 to 15 days old were planted one per pot into 80 × 150 mm pots containing two parts sandy loam, one part vermiculite and one part perlite with controlled release fertilizer ('Nutricote', Chisso Asahi Co. Ltd, Tokyo, Japan) at the recommended rate. There were 10 replicates × 2 species × 2 treatments (16/14°C and 25/15°C). Otherwise growth cabinet conditions were as for the germination trials except for a 14 hr photoperiod. The seedlings were moved into the cabinets after four weeks at 25/15°C. None was given a support to climb on. All plants were dry-weighted at 105°C at an age of 18 wk.

Results and discussion

For all plants of both species introduced to 16/14°C, shoot growth rapidly slowed and then stopped. By contrast, 25/15°C produced rapid growth, with shoot length more than twice as long in *Rhyncharrhena* but shoot dry weight very similar in both species (Table 2). At 18 weeks, the *Marsdenia* seedlings at 25/15°C already had a well-developed tuberous root system while *Rhyncharrhena* had much thinner, non-tuberous roots. This difference correlated with much higher *Marsdenia* root dry weight which in turn resulted in higher total dry weight for that species (Table 2). While *Marsdenia* root weight increased 6.5 times from 16/14°C to 25/15°C, *Rhyncharrhena* increased less than twice. At 16/14°C the tubers of *Marsdenia* were very poorly developed. How this relates to climate and drought survival in the field requires further work.

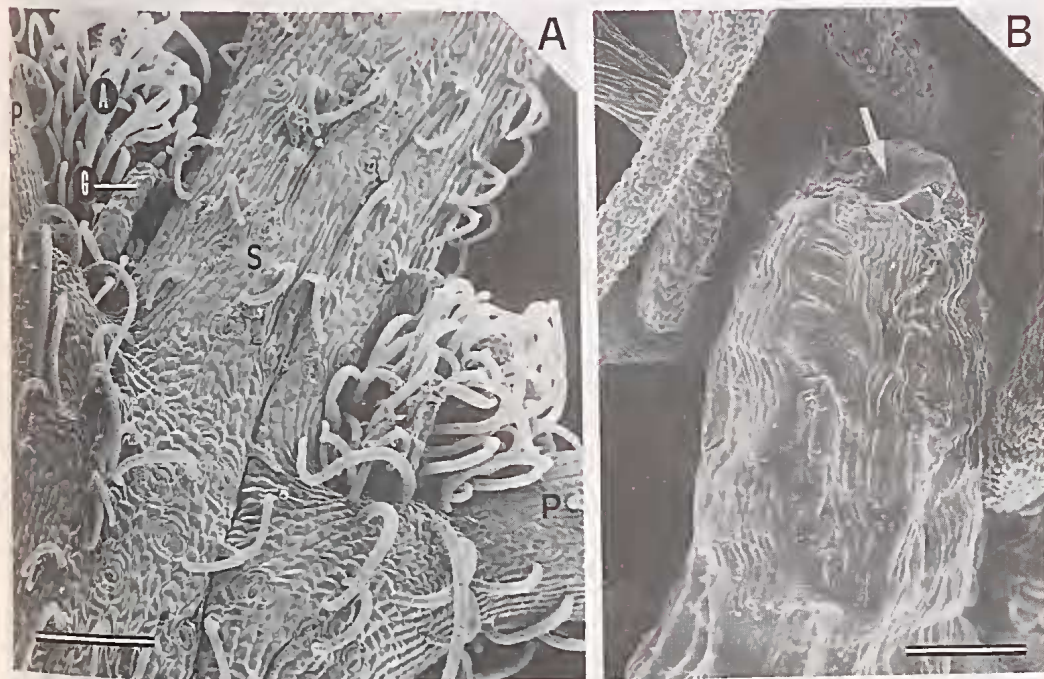


Fig. 11 A, scanning electron micrograph of a *Rhyncharrhena linearis* node, showing stem (S), petiole (P), axillary bud (A) and foliar gland (G). Scale = 0.03 mm. B, head of gland showing pore (arrowed). Scale = 0.3 mm.



Fig. 12. A, longitudinal section through a stem node of *Rhyncharrhena linearis*, showing stem (S), petiole (P), an axillary bud (A) and a foliar gland (G) on the base of the opposite petiole. Scale = 0.2 mm. B, transverse section through a similar node, showing stem (S), axillary bud (A) and foliar gland stalk (G). The petiole (P), cut obliquely, has a crescent-shaped vascular strand (V) and accessory bundles (B). Note the radial arrangement of cells in the gland. Scale = 0.2 mm.

In summary, there are striking differences in seedling growth between the two species. The extra dry matter produced by *Marsdenia* is used for production of tuberous roots. Despite very similar shoot dry weights, *Marsdenia* produces thicker stems, larger leaves and a more rigid, erect shoot while *Rhyncharrhena* produces much longer, thinner shoots (Fig. 15). The reasons for these differences are obscure given the similarity between the two species in behaviour and habitat in the field.

The cessation of growth of both species at 16/14°C is like the behaviour of C₄ grasses at such temperatures (Evans et al. 1964). Given

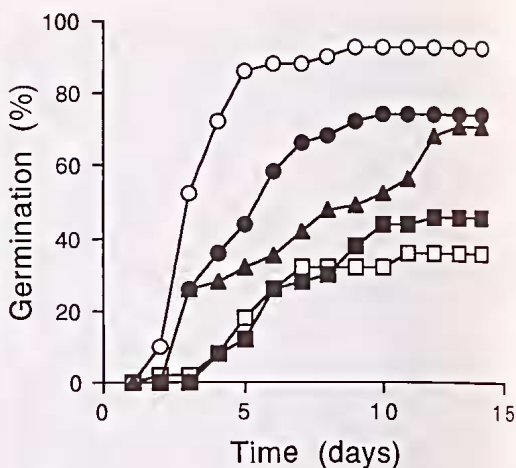


Fig. 13. Germination rate of *Marsdenia australis* and *Rhyncharrhena linearis* at various temperature regimes for seed 19 mo old. Open circles = *Rhyncharrhena* at 25/15°C, open squares = *Rhyncharrhena* at 16/14°C. Closed triangles, circles and squares = *Marsdenia* at 30/20°C, 25/15°C and 16/14°C respectively.

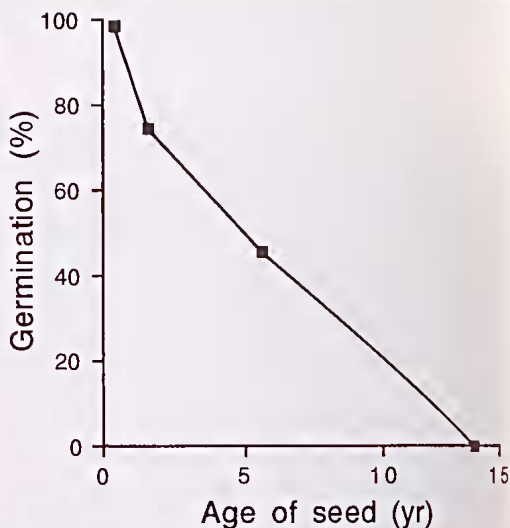


Fig. 14. Germinability of *Marsdenia australis* seeds of various ages at 25/15°C.

that the mean daily maximum temperature in June is about 16°C, the data suggest that little or no growth will occur in winter in the field. This is discussed further below.

These unsupported seedlings bowed over and grew more-or-less horizontally once they reached heights of 150 mm or so. We lack data

	<i>Marsdenia</i>		<i>Rhyncharrhena</i>	
	16/14°C	25/15°C	16/14°C	25/15°C
Shoot length (mm)	66	436	199	1142
Dry weight (g)				
Shoot	0.14	1.57	0.15	1.58
Root	0.29	1.89	0.38	0.71
Total	0.43	3.46	0.53	2.29

Table 2. Mean shoot length and dry weight of 18 wk old *Marsdenia australis* and *Rhyncharrhena linearis* seedlings at two temperature regimes.

for supported young plants except for a single *Marsdenia* plant which twined 1.1 m up a stake in 10 weeks. Possible effects on growth caused by provision of support need investigating.

PHENOLOGY

Methods

General observations were made at all sites. At site 1, from 13 February to 23 May 1990, effects of water supply on shoot growth and flowering were studied by watering two *Marsdenia* and three *Rhyncharrhena* plants with a total of 600 L per plant via 22 L containers feeding a dripper system running at 400 mL/hr. Watering stopped

in May when rainfall had clearly provided available water in the topsoil. Six unwatered control plants were monitored per species.

At site 2, from 19 February to 6 April 1990, one *Marsdenia* and three *Rhyncharrhena* were given 150 L of water each. One *Marsdenia* and three *Rhyncharrhena* were monitored as unwatered controls.

All plants monitored at sites 1 and 2 were more than 0.8 m high and were supported by shrub canopies. From 2 to 6 shoots per plant were tagged initially. Shoots were monitored until September 1990. Unfortunately it was logistically impossible to provide continuous watering to a larger number of plants. This factor, plus death of and damage to some shoots, produced very low replication in some cases, reducing the value of the experiment. Only a summary of the results is given below.

Results

Flowering and fruiting. Observations in the Red Cliffs district on similar numbers of plants of each species from 1981 to 1990 gave a flowering time range of October to March for *Marsdenia* and February to May for *Rhyncharrhena*. For the latter, however, buds can sometimes be seen even in July and September and we think it likely that flowering can occur from October to May (see also Cunningham et al. 1981, Jones & Gray 1988). In general, flowering for both occurs in the warmer months, especially when significant rain has fallen previously. However, *Marsdenia* is more likely to exhibit plentiful general flowering in December–January under a wide range of rainfall regimes. *Rhyncharrhena* seems to have a less definite flowering period; it seems more opportunistic, reacting more quickly with vigorous growth and flowering after significant summer–autumn rains. This species difference is dealt with more fully below. The smallest plants of both species seen flowering were about 600 mm high.

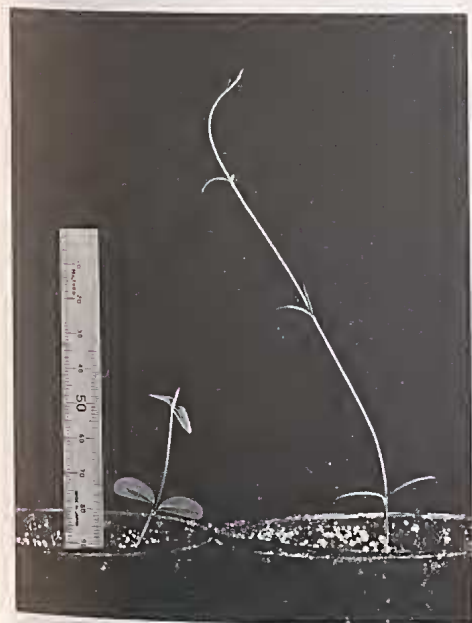


Fig. 15. Seven-week-old seedlings of *Marsdenia australis* (left) and *Rhyncharrhena linearis* (right) grown in a growth cabinet at 25/15°C.

It is much more common for flowers of both species to wither and fall than to produce fruit; this can happen to *Rhyncharrhena* when *Marsdenia* is still flowering and fruiting at the same site. Although *Rhyncharrhena* flowered a number of times from 1981 to 1990, only five fruits (containing a total of 177 seeds) could be found, one in 1982 and four in 1989–90. Other than this, the only *Rhyncharrhena* fruiting records we know of are: (a) June 1950, after exceptional February–March rainfall of 177 mm (E. Ramsay, unpublished manuscript); and (b) March 1976, after exceptional October–December rainfall of 225 mm (our data). Finding as many as four fruits in 1989–90 was not due to heavy rain but because we started to examine repeatedly 48 adult plants; (a) and (b) above may indicate that appreciable levels of fruiting only follow exceptional rains.

Marsdenia fruiting is more common; for example 18 fruits could be found in 1984 and in 1990 38 adult plants under observation produced 15 fruits.

Number of seeds per fruit ranged from 37 to 213 for *Marsdenia* and 18 to 78 for *Rhyncharrhena*. Individual *Marsdenia* flowers remain open for seven to ten days and those of *Rhyncharrhena* for two to three days. This compares with five to six days for *Asclepias meadii* (Betz 1989), seven to eight days for *A. inberosa* (Wyatt 1981) and 10–15 days for *Fischeria funebris* (Skutch 1988).

General phenology, 1989–1990. Following rain falls of 125 mm from 14 March to 7 April 1989, *Rhyncharrhena*, but not *Marsdenia*, flowered in mid-April. Virtually all these flowers were shed in late April without setting fruit.

No further flowering of either species occurred until above-average rain of 54 mm from 6 November to 2 December. By 14 December, shoot growth and flowering occurred profusely in all full-grown *Marsdenia* plants but not in any *Rhyncharrhena* plants.

In this area, 10 mm is the minimum rainfall that most farmers regard as being significant for plant growth in summer. There were no falls this large between 3 December 1989 and 21 April 1990. On 2 January 1990, with temperature maxima about 40°C, all *Rhyncharrhena* plants were either wilted or had started losing leaves. This was not true of *Marsdenia* except for some wilted sucker shoots. However, on 3 January 1990 temperatures reached 47°C, the hottest for 50 years; nearly all *Marsdenia* wilted and shed

their flowers except for those at site 3. The plants at site 3 shed most of their flowers a few days later. By 11 January, most *Marsdenia* shoots had recovered without damage. Between then and 25 January new shoot growth was noted for *Marsdenia* but not for *Rhyncharrhena* which showed further leaf loss and stem death and did not recover until April.

It was possible to obtain a few mature fruits of both species in January 1990; those of *Rhyncharrhena* probably arose from the April 1989 flowering while the origin of the *Marsdenia* fruits is unknown.

Detailed studies. At site 1, small flower buds were present on some plants of both species, especially *Rhyncharrhena*, before watering started. A second crop of *Rhyncharrhena* buds was present on 15 May following substantial rains. Despite these buds, throughout the work only a single plant of either species was seen with open flowers, a *Rhyncharrhena* in early March, and no fruit was set. Plants of both species, both watered and unwatered, showed some increase in shoot length and leaf number from February to September. This was most marked during April and May. The overall increases in mean shoot length to 4 August 1990 were: *Rhyncharrhena* (watered) 473 mm, *Rhyncharrhena* (unwatered) 133 mm, *Marsdenia* (watered) 197 mm and *Marsdenia* (unwatered) 229 mm. Although there was no statistically significant effect of watering, more data may have confirmed that *Rhyncharrhena* responds more strongly to watering than *Marsdenia*.

Events at the other sites from February to September 1990 were generally similar to those at site 1. The very few *Rhyncharrhena* that flowered included two plants at site 2 on 22 March, possibly in response to the artificial watering. The only *Marsdenia* to flower were three plants at site 5 on 6 March following 17 mm of rain. Despite the widespread *Marsdenia* flowering of December 1989, only at site 3 did fruit set occur, with a total of 10 fruits. A fruit cut open in June contained only immature seeds, while seeds from one cut open in August gave 100% germination. The remaining fruits finally opened naturally in mid-November 1990. This period of 11 months from flowering to seed release compares with two to four months from flowering to fruiting for *Sarcostemma esculentum* and *Gynmema geminatum* (Forster 1989) and about 3.5 months from pollination until fruits are ripe in *Asclepias meadii* (Betz 1989).

The period from pollination to seed release for three species of *Asclepias* ranges from about 2 to 4.5 months (Kephart 1987).

With increasing temperatures in September, most mature *Marsdenia* and *Rhyncharrhena* plants produced new crops of flower buds. The driest spring on record ensued (15 mm of rain at Mildura) and December was also very dry (4 mm). All *Rhyncharrhena* flower buds were lost but *Marsdenia* showed widespread flowering by mid-November. With very high January rainfall (87 mm), some flowers produced a crop of fruits 5 mm in diameter by 12 January and these became virtually full-sized by 2 February. A total of 49 full-sized fruits were counted at sites 1 and 3 on 13 February 1991.

By contrast, it was only after the 29 mm of rainfall on 5 January that *Rhyncharrhena* flowered (Fig. 16). It is assumed that this flowering produced the 20 well-developed fruits found at site 1 on 11 February. In central Australia, for both species, "significant fruiting only occurs after exceptional seasons or after fire" (P. K. Latz, personal communication).

The timing of events in *Marsdenia* is consistent over large areas; around Lindsay Point, 115 km to the west-north-west, *Marsdenia* also shed its seeds and flowered in November 1990 (R. Stoeckel, personal communication).

A major difference between *Marsdenia* and *Rhyncharrhena* is that in hot, dry periods during summer and autumn 1990 virtually all *Rhyncharrhena* plants lost at least some of their leaves, while no *Marsdenia* plants did. This was even more noticeable in the very dry late spring of 1990 when the few remaining *Rhyncharrhena* leaves were yellow and wilted while all *Marsdenia* leaves were still present and in good condition. The partial deciduousness of *Rhyncharrhena* may aid survival during drought (Russell-Smith & Dunlop 1987). While *Marsdenia* is regarded by Pate & Dixon (1982) as semi-deciduous if drought-stressed, we have never seen leaf loss at any time. Perhaps leaf loss occurs only in the most extreme conditions, possibly as a prelude to stem death (P. K. Latz, personal communication).

Although it is said that *Rhyncharrhena* can be

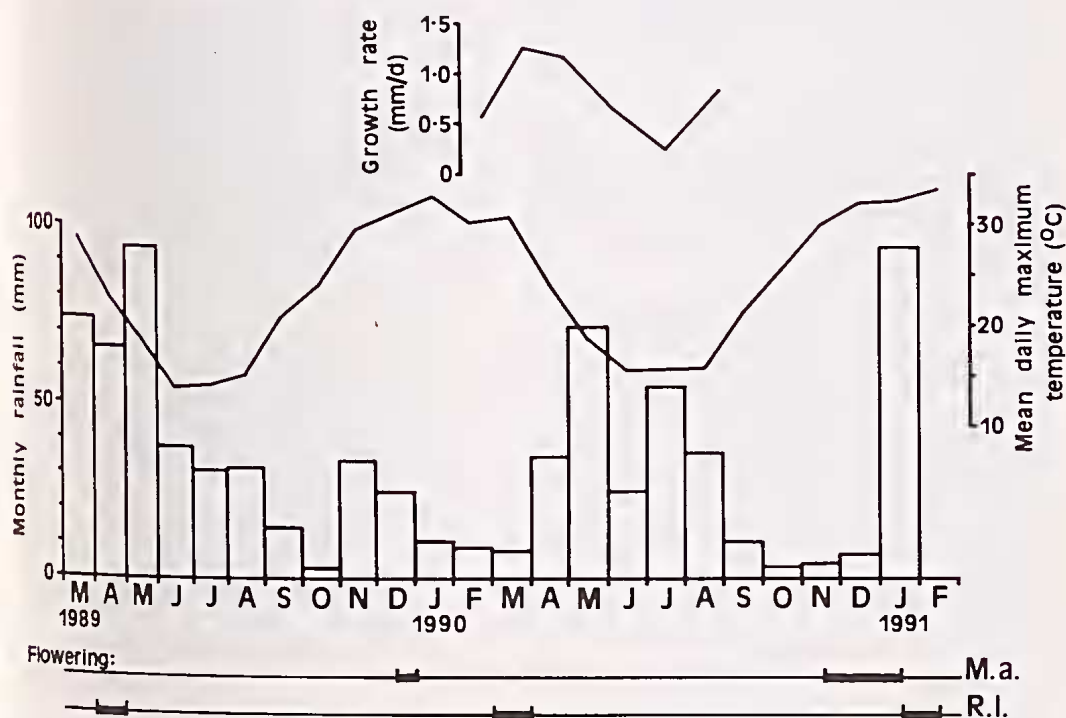


Fig. 16. Monthly rainfall (Red Cliffs), monthly means for daily maximum temperatures (Mildura), flowering times for *Marsdenia australis* and *Rhyncharrhena linearis*, and growth rate (shoot elongation) for unwatered *R. linearis* shoots at site 1 from February to September 1990.

short-lived in cultivation (Jones & Gray 1988), one of us (JHB) has observed individual plants of both species at Red Cliffs for more than 20 years. There has been no apparent size increase. It is possible that such plants may be very long-lived like those of other clonal species (Janzen 1975).

Discussion

Our observations suggest that some shoot growth occurred throughout the February–August period but that this was slow at the start and the finish, presumably due to low soil moisture and low temperatures respectively. Presumably shoot growth stops completely in very dry conditions like November–December 1990. Shoot growth is clearly much more vigorous in summer after thunderstorms or general rain than at other times.

In colder areas of southern Australia, introduced species of *Asclepias* are said to “die back when (night) temperatures drop below 0°C” and so to “disappear over winter” (Zalucki 1986). In our 1990 work, *Marsdenia* and *Rhyncharrhena* did not show any frost damage in a winter when the lowest absolute minimum screen temperature at Mildura was –1°C. Both are said to be tolerant of light to moderate frosts (Jones & Gray 1988). However, for *Marsdenia*, “foliage may dry off after frosts” (Griffin 1985), and in the winter of 1985 plants of both species growing on a fence at Sunny Cliffs showed frost damage while *Marsdenia* plants growing inside shrubs nearby were unaffected (personal observations).

The two species were strikingly different in flowering behaviour. In *Marsdenia* flowering (and fruiting) occurs on a much higher proportion of plants than in *Rhyncharrhena*. There was regular November–December flowering of *Marsdenia*, even in very dry conditions, whereas *Rhyncharrhena* flowering only followed heavy rain. It is not known why heavy autumn rain can produce flowering of *Rhyncharrhena* but not *Marsdenia*, as in 1989. In Queensland rainforest “almost all liane species flower once a year, in early summer” (Hegarty 1988). If individual *Marsdenia* plants flower annually, summer flowering would mean that few or no plants would flower in the succeeding autumn. Neither species flowers or fruits in the cold conditions of winter; it seems that amount of fruiting is related to rainfall at other times, especially summer. For both species, rainfall can be sufficient to produce flowering but be insufficient for any subsequent fruiting to occur.

Marsdenia flowering phenology was categorized by Pate & Dixon (1982) as “flowers produced annually during growth season”.

It was hoped that artificial watering would produce widespread flowering and even fruiting, at least of *Rhyncharrhena*, but it only contributed to very limited flowering of that species. Watering a few shoots might not produce marked changes if those shoots were part of a very large clone covering most or all of the site, as is quite possible.

For both species, large numbers of sucker shoots up to 300 mm high can appear in open areas adjacent to mature plants. This is especially true in wet years like 1974–5, but plenty were found also in 1990 (Table 1). Before site 4 was fenced, *Rhyncharrhena* sucker shoots were grazed right off for three successive years, probably by kangaroos (T. Dominelli, personal communication). However, in unstocked areas near Red Cliffs lacking kangaroos and rabbits, large numbers of *Rhyncharrhena* suckers can appear after rain and then totally disappear during dry conditions, as they did in December 1990. In *Marsdenia*, only the smallest suckers die off during drought.

Most such suckers are found in open areas, often on perennial grasses or on live or dead annuals, but also in completely bare areas. In *Marsdenia*, such suckers can remain small but be many years old. For both species, in the absence of a substantial aerial support the suckers remain as small single shoots or die back; they do not form large, mature plants of shrub or creeper growth form, unlike *Jasminum didymum* (Cunningham et al. 1981, Hegarty & Clifford 1984).

Casual observations of supported and unsupported seedlings (see seedling growth section above) suggest the potential for very rapid height growth responses to provision of support, as is the case for rainforest lianes (Putz 1984).

Some of the striking phenological differences between *Marsdenia* and *Rhyncharrhena* may be because storage material in the tuberous roots of *Marsdenia* allows it to flower, fruit and retain leaves in conditions too dry for such behaviour in *Rhyncharrhena*. Work is needed to compare the water potential and intrinsic cellular resistance to desiccation of both species.

FLORAL BIOLOGY

Despite repeated observations, pollinators could not be found visiting flowers of either species. *Rhyncharrhena* is one of a number of asclepiads which has dark purple flowers (Good

1956). This feature and the presence of vibratile hairs on the flowers suggests that pollination may be by flies (Whittington 1989). Both *Marsdenia* and *Rhyncharrhena* flowers are odourless, at least in daytime.

All species in the family Asclepiadaceae studied in detail are obligate or nearly obligate outbreeders and exhibit low rates of fruit set, typically one to five per cent (see e.g. Holm 1950, Woodson 1954, Skutch 1988). These low rates can be related to low pollination rates and to energy limitation causing abscission of pollinated flowers and pod abortion (see e.g. Cabin et al. 1991, Pleasants 1991). Low rates of fruit set certainly apply also to *Marsdenia* and *Rhyncharrhena*. For a threatened prairie species of *Asclepias* now restricted to a few tiny refugia surrounded by farmland, problems may arise from (a) low populations of insect pollinators, and (b) insufficient plants to attract pollinators and maximize cross-pollination. Problem (b) can be exacerbated by extensive clones of the species causing extensive self-pollination (Betz 1989). These same problems may apply to many isolated *Marsdenia* and *Rhyncharrhena* stands in largely cleared Victorian areas.

Work on *Asclepias quadrifolia* shows that plants under the threshold of 330–340 mm stem height are unable to mature a fruit, any fruits initiated being aborted. Many small flowering plants apparently lack the energy resources to mature a fruit; only 20% of the flowering plants produce a fruit, production of which clearly depletes the plant's energy reserves (Chaplin & Walker 1982). *Marsdenia* and *Rhyncharrhena* seem to exhibit similar behaviour.

RESPROUTING

Fifty days after germination, ten plants each of *Marsdenia* and *Rhyncharrhena* were cut off below the cotyledons. Eight *Marsdenia* plants and all the *Rhyncharrhena* plants had resprouted 14 days later. Similarly, resprouting can occur in cut off 21-day-old *Asclepias syriaca* seedlings (Bhowmik & Bandeen 1976).

Patches of *Marsdenia* are known to persist in some areas of Victoria cleared of native vegetation in the 1920s; the small sucker shoots are repeatedly destroyed by ploughing or stock grazing but new ones continue to be produced by resprouting (J. N. Macfarlane, personal communication). Similar behaviour occurs in asclepiad weeds like *Asclepias syriaca* (Bhowmik & Bandeen 1976) and *Morrenia odorata* (Tucker & Phillips 1974). Such resprouting behaviour also

means that *Marsdenia* and *Rhyncharrhena* can occasionally be found climbing among the trees in commercial citrus groves, where irrigation can cause them to fruit prolifically (J. N. Macfarlane personal communication). Analogously, the asclepiad *Morrenia odorata* is a major weed of Florida citrus groves (Tucker & Phillips 1974).

Post-fire behaviour of *Marsdenia* and *Rhyncharrhena* has not been seen in Victoria. In central Australia, vigorous resprouting can make both species conspicuous after fire, they being among the first species to appear. Later in the post-fire period, increased competition from other perennial species can make them less conspicuous and reduce or prevent their fruiting (Latz 1982 and personal communication). Resprouting allows other asclepiads to tolerate frequent low-intensity fires in monsoon areas further north (Russell-Smith & Dunlop 1987).

RESPONSES TO GRAZING

The Asclepiadaceae is noted for presence of toxic cardiac glycosides, alkaloids and resinoids. As a result, many species are extremely unpalatable to grazing mammals and are generally avoided by them (Everist 1974). For example, severe overgrazing by goats can produce monospecific communities of the poisonous asclepiad *Calotropis procera* (Kassas 1966). Despite this, it is thought that mammal grazing can dramatically reduce *Marsdenia* and *Rhyncharrhena* populations. In Victoria, by 1937 *Marsdenia* was "rapidly becoming rarer" because it was especially palatable to rabbits, which ate the foliage and removed the bark from stems near the ground (Zimmer 1946).

Both species are now very rare virtually throughout their former range in Victoria (see Table 1). For example, only two adult plants of *Marsdenia* are now known in Hattah-Kulkyne National Park and there are only three recent records from the whole of the Sunset Country. The only populations of any size are from unstocked areas close to towns (sites 1 and 3, Red Cliffs; site 5, Walpeup) where rabbit (and other grazing mammal) numbers remain low, possibly due to factors like predation from domestic cats and dogs. *Rhyncharrhena* behaves similarly (Table 1). In some parts of the ranges of both species, grazing by hares may be more important than that by rabbits (J. N. Macfarlane personal communication).

In western New South Wales *Rhyncharrhena* is grazed readily by sheep. Under grazing "the

only plants which appear to survive are those which have the stem closely pressed to the bark of a tree or are growing up through a groove in the bark" (W. E. Mulham, personal communication). In central Australia *Marsdenia* is noticeably rarer in the area of highest rabbit numbers, namely the south west corner where rabbit grazing has apparently severely reduced the species (Latz 1982).

A similar case of a marked grazing effect on a liane concerns the eastern Victorian *Parsonsia brownii* in the closely related family Apocynaceae. *P. brownii* is especially palatable to wallabies and normally only scattered plants of it can be found. Where wallabies are absent, however, as in some very small remnants of native vegetation or in reserves surrounded by suburbs, dense stands of *P. brownii* develop (Ashton 1989; N. H. Scarlett, personal communication). The New Zealand *P. heterophylla* is especially palatable to a browsing bird (Clout & Hay 1989).

DISPERSAL

Both *Marsdenia* and *Rhyncharrhena* have typical asclepiad seeds with a terminal coma of long hairs. In *Asclepias syriaca*, these hairs allow wind dispersal at distances of up to 150 m and further (Morse & Schmitt 1985), and in *Araujia sericifera* such dispersal allows the species "to arrive in almost every Auckland garden" (Esler 1988). There is no evidence that *Marsdenia* or *Rhyncharrhena* seeds are predated by birds or ants.

CONSERVATION

While not threatened Australia-wide, both *Marsdenia* and *Rhyncharrhena* are now regarded as vulnerable in Victoria (Gullan et al. 1990). The apparent severe decline under grazing, the absence of seedling establishment, the lack of information on the lifespan of the remaining adult plants and the very small number of adults in biological reserves are all causes for concern. Although *Rhyncharrhena* is recorded from a total of four Victorian reserves (Beaglehole 1979), in each case only a few plants are present (A. C. Beaglehole and J. N. Macfarlane, personal communications). *Marsdenia* is a very similar case, being regarded even in 1937 as "likely to become extinct" (Zimmer 1946).

Conservation work so far has involved fencing small patches of both species at Hattah-Kulkyne

National Park (site 4) and Pink Lakes State Park (site 6), and at the latter providing small tree guards about 300 mm high for *Rhyncharrhena* suckers. We only saw fruiting of either species occur when the plants were climbing in shrubs or trees; although increased shoot growth occurred when the tree guards were installed, no fruit was set. Grazing exclosures for the species should include long-lived trees or shrubs if possible; if none are present, it may be necessary to introduce them to make the exclosure worthwhile in the long-term.

ETHNOBOTANY

In central Australia *Marsdenia* and *Rhyncharrhena* were important and favoured aboriginal foods, all parts being used except the stems and fine roots. The aborigines were aware that a diet containing a high proportion of *Rhyncharrhena* caused their children to lose weight (Latz 1982). The ground-up seeds of both species are reputed to have been used as an oral contraceptive (Lassak & McCarthy 1983).

The immature fruits of *Marsdenia* are so delicious that the species may be worthwhile cultivating (Cherikoff & Isaacs, no date; V. Cherikoff, personal communication).

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APPENDIX 1

Location of the study sites; see also Table 1.

Site 1. 34°20'S, 142°20'E. All plants studied were less than 50 m W of Campbell Avenue. *Rhyncharrhena* sites on ridge 0.3 km N of 22nd Street. *Marsdenia* sites on ridge 0.3 km farther N.

Site 2. 34°21'S, 142°21'E. W side of main N-S track through reserve, 0.1–0.3 km SE of the intersection of the track and Woomera Avenue.

Site 3. 34°48'S, 142°17'E. S side of Nardoo Street, Red Cliffs. The plants are scattered through the least disturbed area.

Site 4. 34°48'S, 142°17'E. (a) *Marsdenia*. Plot 0.6 km along Jasmine Track from its N end, then 0.2 km WSW of track. (b) *Rhyncharrhena*. National Parks Service plot no. 9E, 0.8 km along Jasmine Track from its N end, then 28 m W of track.

Site 5. 35°10'S, 142°2'E. In the western block of the reserve, 0.5 km S of Ouyen Highway down W boundary track just E of where it meets E–W track.

Site 6. 35°1'S, 141°45'E. (a) *Marsdenia*. Plot near SE corner of Lake Crosby, 0.2 km along Campground Track from its S end, on NE side of track. (b) *Rhyncharrhena*. Plot near S tip of Lake Kenyon, 0.5 km along Lake Kenyon Track from its W end.

APPENDIX 2

Seed sources used

- a) The germination/seed age trial (all *Marsdenia*).
 1. 22 June 1976. Huckitta Station, Northern Territory.
 2. 30 October 1984. Railway and road reserve on W side of Calder Highway where it meets 22nd Street, about 4 km N of Red Cliffs.
 3. 22 October 1988. As for 2 above.
 4. 27 January 1990. Site 1 (Appendix 1).
- b) The germination/temperature trial used no. 3 above and the seedling growth trial used no. 4. All *Rhyncharrhena* seeds used were collected at site 1 (Appendix 1) on 25 January 1990.